

Zusammenfassung

Markierungsangstudien an einer Population der Mittelmeer-Kleinwühlmaus (*Microtus duodecimcostatus*) in Südfrankreich

Eine Population der Mittelmeer-Kleinwühlmaus (*Microtus duodecimcostatus*) wurde in Südfrankreich über einen Zeitraum von 2 Jahren durch Fang, Markieren und Wiederfang untersucht. In Abständen von 3 Monaten wurden Fänge in einem Apfelfgarten auf einer Fläche von 1 ha durchgeführt. Pro Fangtermin wurden 100 bis 400 Individuen gefangen, am wenigsten im Sommer. Die Reproduktion fand das ganze Jahr über statt, war aber im Winter am geringsten. Eine Erneuerung der Population fand insbesondere im Herbst statt. Einzelne Individuen nahmen nicht an der Fortpflanzung teil. Sefthafte Individuen hatten eine längere Lebensdauer und ihr Aktionsraum blieb sehr konstant. Das Durchschnittsgewicht variierte nur bei Weibchen in Abhängigkeit von der Reproduktionsrate. Die beobachtete Demographie von *M. duodecimcostatus* kann durch biologische (Wurfgröße, Lebensdauer) und ökologische Merkmale (hohes und regelmäßiges Nahrungsangebot, geringes Störungsniveau) erklärt werden und weist darauf hin, daß das Sozialverhalten ein wichtiger Regulationsfaktor für die Populationsgröße sein könnte.

References

- ARMITAGE, K. B. (1987): Social dynamics of mammals: reproductive success, kinship and individual fitness. *Trends Ecol. Evol.* **2**, 279–284.
- CHALINE, J.; BRUNET-LECOMTE, P.; GRAF, J.-D. (1988): Validation de *Terricola Fatio*, 1867 pour les Campagnols souterrains (Arvicolidae, Rodentia) paléarctiques actuels et fossiles. *C. R. Acad. Sci., Paris, Sér. III* **306**, 475–478.
- CLARAMUNT, P. T. (1976): Sobre la actividad sexual de *Pitymys duodecimcostatus* de Sélvs-Longchamps, 1839, en Cataluña. *P. Dept. Zool.* **1**, 47–54.
- COHEN-SHLAGMAN, L.; YOM-TOV, Y.; HELLWING, S. (1984): The biology of the Levant vole, *Microtus guentheri* in Israel. I. Population dynamics in the field. *Z. Säugetierkunde* **49**, 135–147.
- CORBET, G. B.; HILL, J. E. (1991): A world list of mammalian species (3rd Ed.). *Nat. Hist. Mus. Publ., Oxford Univ. Press.*
- CORNBOWER, T. R.; KIRKLAND, G. L., Jr. (1983): Comparisons of pine vole (*Pitymys pinetorum*) populations from orchards and natural habitats in southcentral Pennsylvania. *Proc. Pa. Acad. Sci.* **57**, 147–154.
- DUNBAR, R. I. M. (1985): Population consequences of social structure. In: *Behavioral ecology: ecological consequences of adaptive behaviour*. Ed. by R. M. SIBLY and R. H. SMITH. Oxford: Blackwell Scient. Publ. Pp. 507–519.
- GUEDON, G. (1987): Influences de diverses spéculations et pratiques culturelles sur certains paramètres de la cinétique de populations de campagnols à douze côtes, *Pitymys duodecimcostatus* (de Sélvs-Longchamps, 1839) dans le Montpellierais (France). D.E.A. report, Univ. Montpellier II.
- GUEDON, G. (1988): Cinétique de population de *Pitymys duodecimcostatus* dans le Montpellierais (France). *Bull. OEPP* **18**, 453–461.
- GUEDON, G.; BELAIR, M.; PASCAL, M. (1990): Comparaison de l'efficacité de cinq pièges non vulnérants à l'égard de la capture du Campagnol provençal (*Pitymys duodecimcostatus* de Sélvs-Longchamps, 1839). *Mammalia* **54**, 137–145.
- GUEDON, G.; PASCAL, M. (1992): Eléments de validation d'une méthode d'échantillonnage linéaire standardisée adaptée au Campagnol provençal (*Pitymys duodecimcostatus* de Sélvs-Longchamps, 1839). *Rev. Ecol. (Terre Vie)* **47**, 85–102.
- GUEDON, G.; PASCAL, M.; MAZOUIN, F. (1991a): Le campagnol provençal en captivité (*Pitymys duodecimcostatus* de Sélvs-Longchamps, 1839) (Rongeurs, Microtidés) I. La reproduction. *Mammalia* **55**, 97–106.
- GUEDON, G.; PASCAL, M.; MAZOUIN, F. (1991b): Le campagnol provençal en captivité (*Pitymys duodecimcostatus* de Sélvs-Longchamps, 1839) (Rongeurs, Microtidés) II. La croissance. *Mammalia* **55**, 397–406.
- HENDRICH, H. (1983): On the evolution of social structure in mammals. In: *Advances in the study of mammalian behavior*. Ed. by J. F. EISENBERG and D. G. KLEIMAN. *Spec. Publ. Amer. Soc. Mammal.* **7**, 738–750.
- HONACKI, J. H.; KINMAN, K. E.; KOEPL, J. W. (1982): *Mammal species of the world: a taxonomic and geographic reference*. Lawrence, Kansas: Allen Press.
- INNES, D. G. L. (1978): A re-examination of litter size in some North American microtines. *Can. J. Zool.* **56**, 1488–1496.
- KELLER, B. L. (1985): Reproductive patterns. In: *Biology of New World Microtus*. Ed. by R. H. TAMARIN. *Spec. Publ. Amer. Soc. Mammal* **8**, 725–778.
- KREBS, C. J.; BOONSTRA, R. (1984): Trappability estimates for mark-recapture data. *Can. J. Zool.* **62**, 2440–2444.

- LEFEVRE, C. (1966): Etude de la croissance en élevage de *Pitymys duodecimcostatus* de Séllys-Longchamps originaires du Gard. *Mammalia* **30**, 56–63.
- LELOUARN, H. (1974): Etude par marquage et recepteurs du campagnol des champs et du campagnol de Fatio en montagne. *Mammalia* **38**, 54–63.
- LINDQUIST, S. B.; TIPTON, A. R.; YARROW, G. K.; HASBROUCK, J. J. (1981): Analysis of seasonal dynamics of pine vole populations in two Virginia orchards. In: Proceedings of the fifth eastern pine and meadow vole symposium. Ed. by R. E. BYERS. Gettysburg, PA. Pp. 79–83.
- MCGUIRE, B.; NOVAK, M. (1984): A comparison of maternal behaviour in the meadow vole (*Microtus pennsylvanicus*), prairie vole (*M. ochrogaster*) and pine vole (*M. pinetorum*). *Anim. Behav.* **32**, 1132–1141.
- MILLER, D. H.; GETZ, L. L. (1969): Life-history notes on *Microtus pinetorum* in central Connecticut. *J. Mammalogy* **50**, 777–784.
- NIETHAMMER, J. (1982): *Microtus duodecimcostatus* (de Séllys-Longchamps, 1839) – Mittelmeer-Kleinwühlmaus. In: Handbuch der Säugetiere Europas, Bd. 2/I, Nagetiere II. Ed. by J. NIETHAMMER and F. KRAPP. Wiesbaden: Akad. Verlagsges. Pp. 463–475.
- NIETHAMMER, J.; KRAPP, F. (eds) (1982): Handbuch der Säugetiere Europas, Bd. 2/I, Nagetiere II. Wiesbaden: Akad. Verlagsges.
- NOWAK, R. M.; PARADISO, J. L. (1983): Walkers' Mammals of the world (4th Ed.). Baltimore, London: John Hopkins Univ. Press.
- PALOMO, L. J.; VARGAS, J. M.; ANTÚNEZ, A. (1989): Reproduction de *Microtus (Pitymys) duodecimcostatus* (de Séllys-Longchamps, 1839) (Mammalia, Rodentia) dans le sud de l'Espagne. *Vie et Milieu* **39**, 153–158.
- PARADIS, E. (1990): Démographie d'une population de campagnol provençal (*Pitymys duodecimcostatus*): hypothèses sur les mécanismes de régulation en milieu anthropisé. D.E.A. report, Univ. Montpellier II.
- PASCAL, M. (1984): Méthode d'échantillonnage d'un rongeur souterrain, la forme fouisseuse du campagnol terrestre (*Arvicola terrestris scherman*). Recherche des limites d'utilisation de la méthode. *Acta (Ecologica/Ecol. Applic.)* **5**, 303–317.
- PASCAL, M.; MEYLAN, A. (1986): L'échantillonnage linéaire des populations de la forme fouisseuse du campagnol terrestre (*Arvicola terrestris scherman* [Shaw]). Description des techniques. *La Défense des Végétaux* **237**, 3–12.
- PELIKÁN, J. (1973): Notes on the reproduction of *Pitymys subterraneus* (de Sél. Long.). *Zoologické Listy* **22**, 285–296.
- SALVIONI, M. (1986): Domaines vitaux, relations sociales et rythmes d'activité de trois espèces de *Pitymys* (Mammalia, Rodentia). Ph. D. diss., Univ. Lausanne.
- SALVIONI, M. (1988): Rythmes d'activité de trois espèces de *Pitymys*: *Pitymys multiplex*, *P. savii*, *P. subterraneus* (Mammalia, Rodentia). *Mammalia* **52**, 483–496.
- SCHADLER, M. H.; BUTTERSTEIN, G. M. (1979): Reproduction in the pine vole, *Microtus pinetorum*. *J. Mammalogy* **60**, 841–844.
- SIMPSON, D. A.; ANTHONY, R. G.; KELLY, G. M.; STORM, G. L. (1979): Dynamics of a pine vole population in a Pennsylvania orchard. In: Proceedings of the third eastern pine and meadow vole symposium. Ed. by R. E. BYERS. New Paltz, N. Y. Pp. 47–51.
- STAPLES, P. P.; TERMAN, C. R. (1977): An experimental study of movement in natural populations of *Mus musculus*, *Microtus pennsylvanicus*, and *Microtus pinetorum*. *Res. Popul. Ecol.* **18**, 267–283.

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Evaluation of hare abundance allowed by their use of attraction points

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Abstract

Studied the space use by hares (*Lepus granatensis*) which was affected by wooden stakes placed in an open grassland at Doñana Biological Reserve (SW Spain). Densities of hare pellets on plots centered on the stakes were higher than on plots not centered on them. The use of stakes by hares seems to be related either to an anti-predator behaviour or to a social behaviour of ground marking. Neither the time nor spatial variation in hare abundance was related to food supply or to the herbaceous layer characteristics. Rather, the seasonal abundance of hares in the study area depended on the flooding patterns of adjacent plant communities. The use of stakes as an improved version of the pellet-count method is proposed. This modified method considerably reduces the sampling effort necessary to carry out realistic estimations of spatial and seasonal variations in the relative abundance of hares in open fields.

Introduction

The ecology and behaviour of hares of the South Iberian Peninsula (*Lepus granatensis* Rosenhauer) is practically unknown. Their taxonomic status and geographic distribution were described by PALACIOS and MEIJIDE (1979) and PALACIOS (1983), but these aspects have recently been questioned (SCHNEIDER and LEIPOLDT 1983; BONHOMME et al. 1986; CORBET 1986; PALACIOS 1989). These animals live in habitats characterized by a high abundance and diversity of predators (SORIGUER and ROGERS 1979) that can strongly influence their activity pattern and space use.

Among other reasons for the lack of information about this species is the high time-and-monetary cost of the traditional methods for studying lagomorph abundance and its temporal and spatial variation: capture-recapture, road-side surveys and pellet counts (TAYLOR and WILLIAMS 1956; BURNHAM et al. 1980). These methods do not seem to be very suitable for low density populations because of the high sampling effort necessary to obtain realistic estimations.

An alleged behaviour of hares due to the presence of attraction points in an open grassland is described in this study. It allows the application of a new method to estimate spatial and temporal variations of their abundance in open fields at low population densities. Through its application the first information about the seasonal pattern of hare distribution at Doñana Biological Reserve (SW Spain) is given, as well as its relation to environmental variables.

Material and methods

Study area

The Doñana Biological Reserve (37°N, 6°W; SW Spain) is an area with Mediterranean climatic characteristics and a strong seasonality in the temperature and rainfall regimes. Two biotopes can be distinguished mainly within its 67 km²: the salt marsh, and the scrubland on sandy soil (ROGERS and MYERS 1980). The salt marsh is flooded during the winter and spring months (November to May), and remains dry the remainder of the year. Its plant cover is mainly sedges (*Scirpus maritimus* and

Eleocharis palustris), whereas the scrubland shows a high basal cover by browse species (mainly *Halimium* spp., *Stauracanthus genistoides*, and *Erica* spp.). An ecotone zone located between the scrubland and the salt marsh is occupied by communities of herbaceous plants with a floristic composition determined both by the depth of the water level and the soil salinity (ALLIER and BRESSET 1978).

The work was carried out within a plant community of the ecotone zone. The study area is located on sandy-clay soil, between the salt marsh and a *Juncus maritimus* community. The ground is characterized by a complete lack of relief, and is usually flooded during the winter dependent on rainfall. The plant cover is very homogeneous and only small-size forbs and grasses are present. Some representative species are *Plantago coronopus*, *Aeluropus littoralis*, *Hordeum marinum*, *Polypogon maritimus* and *Frankenia laevis*. Plant nomenclature follows VALDÉS et al. (1987).

Pellet counts

In October 1989, 20 pairs of 1 m² plots were fixed in the study area. Each plot in a pair was 10 m away from the other one. Paired plots were numbered in sequence and placed every 20 m along a straight line perpendicular to the line delimited by the two plots in a pair (Fig. 1). A wooden stake, 16 cm² in square-section with its top 30 cm above the ground level was driven at the centre of the right plot of each pair (marked plot). The minimum distance between each stake and the nearest rush bed (JD) was measured with an accuracy of 1 m.

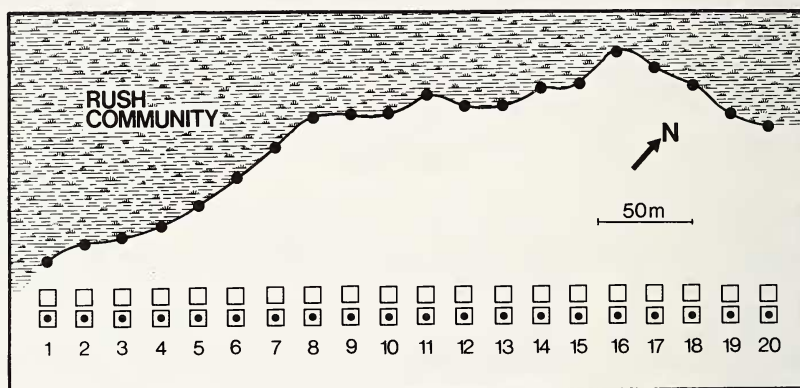


Fig. 1. Location of marked plots (squares filled with a point) and un-marked plots (white squares) in the study area. For clarity, plots appear larger than would be expected according to scale. Black points at the rush community edge do not represent its actual limits but the minimum distance from each stake to the nearest rush bed

From November 1989 to the beginning of March 1990 the study area remained flooded. Monthly pellet counts on the marked plots were carried out from March to September and in November. The number of pellets on each plot (PN) was counted and a mean density of pellets (MDP) was calculated for each month. In the June sampling all the pellets from the odd-numbered plots marked with stakes were removed. Thereafter until the end of July an intensive sampling was carried out (18 counts), the numbers of pellets appearing since the last count being recorded. The average time (\pm s.e.) elapsed between two consecutive counts was 3.59 ± 1.05 days. After each count the pellets were removed only from the odd-numbered plots. Additional pellet counts were carried out on the un-labelled plots in April, June, September and November.

Vegetation sampling

Estimates of the dry biomass availability (DB), the water content of vegetation (HC), the maximum height of green grass (MH), the basal cover of the herbaceous vegetation (SC), the forb contribution to the total cover (FC), and the contribution of dead grasses to the total basal cover of grasses (GC) were obtained monthly. The aerial biomass of the herbaceous layer was estimated on five 0.2 m² plots, fixed regularly along the straight line delimited by the stakes. The pasture samples were weighed with an accuracy of 0.1 g and dried in a hot-air oven at 50 °C until constant weight. The maximum height of

green grass was measured on each labelled plot with an accuracy of 1 cm. Cover estimates were carried out visually on each plot using an ordinal scale (WALKER 1976).

Some data were analysed using non-parametric statistical tests (SIEGEL 1956). A significance level of 0.05 was fixed for all analyses.

Results

Use of stakes

The differences between the mean density of pellets on both marked and unmarked plots were obvious during the entire study period (Tab. 1). Visual inspections of the un-labelled plots did not show different pasture characteristics with regard to the labelled plots, as expected by the short distance between them. Thus, the high number of pellets on the marked plots suggests that the stakes operated as attraction centres for hares.

Table 1. Mean pellet densities \pm s.e. for the marked and the non-marked plots

Pellets were removed from the odd-numbered plots marked with stakes after the counts in June. Thus, only the even-numbered plot counts ($n = 10$) were used for estimating mean pellet density at the marked plots in September

	Marked	(n)	Un-Marked	(n)
Apr	4.80 \pm 1.17	(20)	0	(20)
Jun	32.89 \pm 4.10	(20)	1.25 \pm 0.39	(20)
Sep	6.59 \pm 1.32	(10)	0.80 \pm 0.28	(20)
Nov	24.89 \pm 3.33	(20)	0.15 \pm 0.11	(20)

$n =$ number of 1- m² quadrats

Time variation

The use of the stakes by hares during the study period shows a pronounced seasonal pattern (Fig. 2). In March the sampling was carried out when the area had recently emerged from the winter flood and no pellets were detected on the plots. The maximum pellet densities around the stakes were observed in May, June and July. During the more intensive sampling of the marked plots carried out in the second half of this period, an appearance rate of 0.15 pellets m⁻² day⁻¹ was recorded. From July to September an

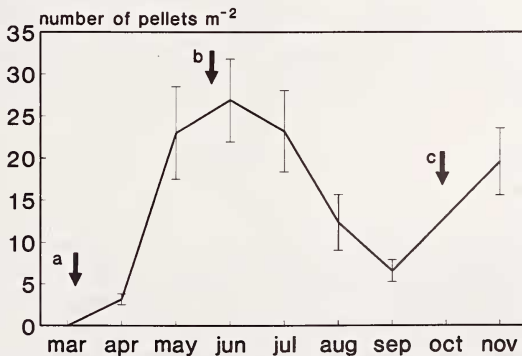


Fig. 2. Changes in the mean density of pellets ($\bar{x} \pm$ s.e.) corresponding to the even-numbered plots of the transect line ($n = 10$). The arrows show: (a) the end of the flooding period at the study area, (b) the end of the flooding period in the marshland and (c) the beginning of autumn rains

important reduction in MDP was observed. In August and September the presence of hares at the study area was verified through the counting of new pellets appearing on the odd-numbered plots marked with stakes. Data for November showed a new increase in the mean density of pellets.

Lag-correlogram between the monthly values of MDP and the mean value of each vegetation variable (DB, HC, MH, SC, FC and GC), both estimated at the marked plots, showed no significant Spearman cross-correlation coefficient ($P > 0.05$ for all correlations).

Spatial variation

Spearman correlation coefficients (r_s) between PN and the vegetation variables estimated on each labelled plot (MH, SC, FC and GC) were calculated for each month. Due to the number of coefficients (28), by chance alone it could be expected that one would be significant under the no relationship hypothesis, and in fact, only one correlation between pasture characteristics and the number of pellets is significant (Tab. 2). However, a relation between the number of pellets and the distance from the stake to the nearest rush bed (JD) was indicated: the correlation coefficients are significant and positive for May, June and July and negative for November (Tab. 2).

Table 2. Spearman correlation coefficients between the pellet number and the vegetation variables estimated on each plot of the marked transect line

	n	MH	SC	FC	GC	JD
Apr	20	-0.074	0.064	-0.138	-0.338	0.102
May	20	0.235	0.384	0.355	-0.363	0.693**
Jun	20	-0.234	-0.122	0.325	-0.032	0.648**
Jul	10	-0.265	0.259	0.526	-0.540	0.748*
Aug	10	-0.345	-0.030	0.108	-0.075	0.480
Sep	10	0.348	-0.686*	0.166	-0.076	0.295
Nov	20	0.064	-0.061	-0.189	0.215	-0.620**

n = number of 1- m² quadrats; MH = maximum height of green grass; SC = basal cover of the herbaceous vegetation; FC = forb contribution to the total cover; GC = contribution of dead grasses to the total basal cover of grasses; JD = minimum distance between the stake and the rush bed. * $P < 0.05$; ** $P < 0.01$

The r_s between the number of new pellets appearing in the odd-labelled plots during the period of continuous sampling and JD showed a related probability very near the significance level ($r_s = 0.642$, $P = 0.054$, $n = 10$). No significant difference was detected between sampling distributions of the number of new pellets appearing in odd and even-numbered plots marked with stakes ($K_d = 0.3$, $P = 0.99$, $n_1 = n_2 = 10$, two-tailed test).

Discussion

VALVERDE (1960) and KUFNER (1986) have pointed out that the salt marsh is the biotope of Doñana with the highest intensity of use by hares in summer and autumn. From November 1989 to June 1990 the salt marsh was flooded. During this period hares would have been forced to occupy the ecotonal areas between the marshland and the scrubland, as VALVERDE (1960) and RAU et al. (1992) suggest. As new areas emerged because of the decrease in the water level, the animals probably moved progressively into the salt marsh. This hypothesis would explain the absence of pellets in March, the slow increase detected subsequently in the mean density of pellets and their progressive decrease from June to

September. Early rains in October, usually responsible for the salt marsh flooding, could again cause the migration of hares towards the highest fields of the ecotone with the scrubland. This could be responsible for the increase in the mean pellet density recorded in November relative to the previous sampling in September. The observed seasonal pattern in hare abundance thus seems to be the result of a "concentration-dilution process" of hare numbers in the study area due to drastic reductions and increases of the available land surface.

The extent of the differences observed between the pellet counts in the marked and non-marked plots shows that stakes have operated as centres of attraction for hares. The accumulations of pellets around the stakes could reflect a ground-marking behaviour as well as an anti-predatory adaptation.

A social behaviour of ground marking through pellet grouping has been described for several lagomorph species. This behaviour is often manifested at points characterized either by their ground elevation or by the existence of easily identifiable landscape elements (BELL 1985). In the study area the stakes break the uniformity of a very homogeneous landscape and appear to be suitable points for the manifestation of such behaviour by hares. Pellet accumulations have been observed in brown hare (*Lepus europeaus* Pallas) ranges, but seem to be more related to the high levels of use of small areas than to the formation of latrines (BELL 1985).

On the other hand, the relevance for lagomorphs of vegetation cover as shelter against predation in Mediterranean environments has been pointed out by JAKSIC and SORIGUER (1981). In the study area diurnal and nocturnal predators of hares (e.g. Spanish imperial eagle *Aquila adalberti*, Iberian lynx *Lynx pardellus* and fox *Vulpes vulpes*) occur at very high densities (KUFNER 1986). Therefore, in the absence of marked relief, high vegetation or relevant rocks, sufficiently large wooden stakes could provide hare shelter from predation. Perhaps the stakes break the hare figure, making it more difficult for predators to detect their prey and also could provide protective elements against direct attacks.

Both hypotheses can explain the significant and positive correlation observed for May, June and July between pellet numbers per plot and distance from the stake to the rush bed; they also explain the absence of a relationship between pellet numbers and the descriptive variables of the herbaceous layer at each labelled plot. Thus, stakes far away from the rush bed would be more attractive as reference elements for ground marking by pellet accumulations. On the other hand, during resting periods hares would use the stakes distant from the rush bed, situated in areas more exposed to predation, at higher frequency. The low use of the area before April and after the draining of the salt marsh can explain the absence of a relation between the pellet number and the distance to the rush bed for the sampling in April, August, and September. The ground level at the rush beds is elevated over the soil level at the plot locations. Thus, the November results could be interpreted in the sense of hares having to use the safe rush beds, and therefore the stakes adjacent to them, with regard to the flooding risk of the area after the first intense rain.

Hares do not show a conspicuous behaviour and commonly are solitary animals, although temporary grouping in feeding areas have been described for brown hare (MONAGHAN and METCALFE 1985) and during the oestrus period for mountain hare *Lepus timidus* (HEWSON and HINGE 1990). For that reason, estimations of their relative abundance with standard methodology are not usually feasible in areas occupied by low-density populations. Based on road-side surveys, time-and-spatial variations in hare abundance are very difficult to quantify because of the large number of visual contacts necessary to carry out the estimations (BURNHAM et al. 1980). Similarly, a large sample size is necessary, either in the number or size of plots, to obtain suitable data for estimating variations in abundance by the pellet count method (TAYLOR and WILLIAMS 1956). The results above suggest that the use of stakes could be a way to improve the pellet count technique reducing the sampling efforts for obtaining adequate sample sizes. This method has not